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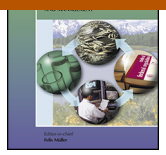

Winners and losers in a long-term study of vegetation change at Moor House NNR: Effects of sheep-grazing and its removal on British upland vegetation

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ABSTRACT

We analysed data collected between 1954 and 2000 from nine long-term experiments designed to assess the effects of sheep-grazing versus no-sheep-grazing at Moor House NNR, an Environmental Change Network site. The experiments were set up between 1954 and 1972 across a range of vegetation types typical of much of upland Britain. Data from this type of experiment are often difficult to analyse and we describe the procedures undertaken to prepare the data for analysis. We fitted the resultant data to the British National Vegetation Classification and used ordination techniques to assess the relative positions of the experiments to each other. Finally, we used Generalized Linear Mixed-effects Modelling within a Bayesian framework to model change of species taxonomic/physiognomic groups through time in both sheep-grazed and ungrazed treatments across all nine experiments; variables included species diversity, Shannon–Weiner index and derived data on occurrence and abundance of species groups based on taxonomy and physiognomy. Hurdle analysis was used to model the species groups; this analysis separated the change through time in both probability of occurrence (binomial distribution) and abundance (Poisson distribution).

In the sheep-grazed plots (the "business-as-usual" treatment hence here designated the "control") there was a reduction in species diversity and a decrease in abundance of vascular plants, grasses, lichens, liverworts and mosses; whereas herbs, sedges and shrubs increased. When probability of occurrence was considered, there was a reduction in number of presences of both lichens and liverworts. Thus, the status quo management of continuous sheep-grazing, even though reduced since 1972, has resulted in a marked change in species composition of these plant communities, with some winners and some losers, but overall they support the concept of biotic homogenization. It is likely that some of these changes were driven by external factors such as elevated atmospheric nutrient deposition. Removal of sheep grazing had some positive benefits; with the herbs, mosses, sedges and shrubs increasing, but faster reductions in grasses and liverworts. Sedges + rushes were stable. It suggested that future monitoring schemes might use either the probability of occurrence of liverworts and lichens, or the abundance of lichens, liverworts, grasses and mosses as sensitive indicators of change in upland Britain.

Moreover, during the period that Moor House has been protected as a nature reserve some key plant species groups have declined in spite of reductions in grazing pressure. To reverse this trend requires some form of interventionist management. In order to increase the diversity of vascular plants some form of disturbance will probably be needed, but for bryophytes and lichens this remains a research question. If the results from these small-scale experiments are replicated at the landscape scale a reduction of sheep grazing pressure, for example in rewilding schemes, will have little effect on species composition over a 28–44 year period.

1. Introduction

In order to manage our natural resources wisely, i.e. in a sustainable way, it is essential to have some understanding of how our ecosystems change through time, and how they respond to

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environmental drivers of change. Such drivers of change might include external factors such as climate change and pollutant loads and internal factors such as land management. Studies linking ecosystem change to environmental drivers are usually done using either a correlative approach, or by direct experimentation. The correlative approach is done most effectively when a large fraction of the available environmental resource has been surveyed and correlated directly to measured changes in the environmental drivers, or some proxy for them. A good example of this approach is the use of data from the Countryside Survey of Great Britain (Haines-Young et al., 2003; Firbank et al., 2003; Smart et al., 2003a; Maskell et al., 2010), where measures of species change indicated that productive species, known to respond to atmospheric nitrogen pollution, were favoured (Smart et al., 2003b; Maskell et al., 2010). The second approach is where vegetation is monitored through time within either permanent plots\transects (Thomas, 1960, 1963) or within experiments where management interventions are compared against an untreated control over a fairly long period; such long-term manipulative experiments are particularly valuable for testing ecological hypotheses (Silvertown et al., 2010). There are many examples of such experimental studies, but there are two main types: the first are experiments that measure the effects of applied treatments in a single location, well-known examples include the early Breckland grass-heath experiments of A.S. Watt (Watt, 1957, 1960a,b, 1962) and more recent ones such as the Buxton Climate Change Impacts Laboratory (Bates et al., 2005; Grime et al., 2008), Cedar Creek Ecosystem Science Reserve (Wilson and Tilman, 1993; Tilman, 1994; Tilman et al., 1994), and the Park Grass Experiment at Rothamsted Experimental Station (Tilman et al., 1994; Silvertown et al., 2006). This type of experiment provides detailed information about the effects of manipulated factors on species change and ecosystem properties. The second type are experiments that consider the effects of similar treatment interventions on the same ecosystem type in a range of locations, extending the assessment of impacts over a greater range of variation of that ecosystem, are particularly valuable. These multi-site studies are less common than those on single sites and are more complex to analyse (Alday et al., 2013; Alday and Marrs, 2014).

The Environmental Change Network (ECN) site at Moor House National Nature Reserve (NNR) provides a third approach where a single treatment has been tested in a range of different plant communities over varying time periods from 28 to 44 years (Adamson and Kahl (2003). This approach was pioneered by A.S. Watt in his studies on grass-heath at Lakenheath Warren where he had similar experiments on a range of plant communities, although he analysed them separately (Watt, 1940). When Moor House was first designated for research work, it was perceived that there was a need for long-term information on the effects of both sheep grazing and its removal across the range of variation in plant communities found on the reserve (ca. 4000 ha). The vegetation comprised a mosaic of different upland plant communities dominated by dwarf-shrubs, grasses or sedges, occurring on soil types ranging from deep blanket peat through to brown-earth soils, and subject to different sheep grazing pressures (Eddy et al., 1969; Rawes and Welch, 1969; Heal and Smith, 1978). Accordingly, between 1954 and 1972 a series of nine experiments with similar designs, and monitored using the same methods (Marrs et al., 1986), were set up to compare the long-term effects on the vegetation of sheep grazing compared to sheep removal. In the early part of the time-series, detailed studies by Rawes and Welch (1969) estimated that there were 15,400 sheep on the Reserve in the summer months, assuming a grazing area of 3500 ha, this averaged 4.4 sheep ha^{-1} across all vegetation types. In 1972, after the formalization of grazing rights for Moor House under the Commons Registration Act (1965), grazing density was more than halved to 7000 sheep or 2 sheep ha^{-1}. From a conservation point of view, it was hoped this reduction would lead to an improvement in vegetation quality.

This suite of nine experiments covered the major moorland vegetation types that are found across the Moor House reserve, and are representative of many upland ecosystems found in much of upland Britain, although many less frequent or regional community-types are not covered (Averis et al., 2004). Some preliminary results have been published on species change in individual experiments, for example the high-level grasslands (Rawes, 1981), two of the blanket bog experiments (Rawes, 1983) and a *Juncus squarrosus*-dominated community (Marrs et al., 1988) but no attempt has been made to produce an holistic analysis. There are several problems in doing such an analysis (Marrs et al., 1988). First, the data from all the individual experiments are unreplicated, with only one sheep-grazed plot and an equivalent ungrazed exclosure in each location. Second, the experiments have been monitored irregularly (between 3 and 8 times), but over a fairly long time period, 28–44 years (Adamson and Kahl, 2003). One way to add power to the analysis is to assess change based on the combined data from all experiments; this approach should provide an overview of change with any significant result being a function of measured change across all experiments. Here, therefore, we provide a combined analysis of change across all nine experiments at Moor House. There are three further complications. The first is that the grazed treatment is the "business-as-usual" condition and hence must be treated as "the control" and the removal of sheep grazing is the applied "intervention" treatment. Clearly, there will be changes in species composition in these "control" plots through time caused by other environmental factors and there have been changes in sheep grazing pressure because of the deliberate reduction in grazing pressure in the early 1970s. The second is that some of the experiments were not monitored from the outset, rather they were set up on "similar, visually identical vegetation". The third issue is that to provide a rigorous assessment we can only assess significant directional change within the grazed plots, i.e. the "controls", and then measure any additional significant change associated with grazing removal, the "intervention-treatment".

There were three parts to this study. The first was to provide a descriptive context for the vegetation in each experiment so that managers could use the results in other locations. We did this by allocating the vegetation in each experiment to a community type within the British National Vegetation Classification (NVC; Rodwell, 1991, 1992). Second, we analysed the data using multivariate analysis so that the relationships between experiments could be assessed. The third part considered the change in abundance of selected taxonomic/physiognomic groups (hereafter termed Groups) through time; these groups were used rather than functional traits, because they are more easily recognizable by conservation managers. We tested the following hypotheses: (1) the null hypothesis was that there would be no directional change in the sheep-grazed plots through time, i.e. there would either be a steady-state or any change could be described as a fluctuation, a change in individual species abundance around a notional mean; (sensu Miles, 1979), (2) if this hypothesis was rejected and a directional change detected this would provide evidence for either (a) conservation enhancement (+ve relationship), or a conservation loss (−ve relationship). If a loss was detected this would support the hypothesis of biotic homogenization that has been reported in upland areas with losses in sub-dominant vascular plants, lichens and bryophytes (Smart et al., 2006; Britton et al., 2009; Ross et al., 2012). Moreover, identification of groups that changed through time in the sheep-grazed plots would provide sensitive indicators that might be used elsewhere to monitor for damaging change. Hypothesis 3 tested whether there was an effect (+ve or −ve) with respect to the removal of sheep-grazing. This might provide indicator groups to inform future conservation policy involving reducing

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or stopping sheep grazing in selected upland areas including the possibility of rewilding (Monbiot, 2013; Sandom et al., 2013).

However, there were two other problems to surmount. First, in common with many ecological studies of this type, the dataset contained a large number of zeros. Second, change in species composition within a plant community can occur either though a reduction in the number of species occurrences, or a reduction in species abundance. We, therefore used hurdle models to identify the effects of sheep grazing versus no sheep grazing through time on both (a) the change in the number of presences/absences (i.e. point occurrences), and (b) changes in abundance when the Group was present. Hurdle models combine a zero-hurdle model with a binomial distribution, and a left-truncated count data model with a Poisson distribution. They have been heavily used in econometrics (Mullahy, 1986; Cameron and Trivedi, 1998, 2005), but they have been rarely applied to data from ecological experiments, despite their obvious potential (Potts and Elith, 2006).

2. Methods

2.1. Experimental design

The nine experiments were located across the Moor House reserve to cover the range of variation in the vegetation across the area, i.e. from relatively productive *Agrostis-Festuca* grassland on brown-earth soils and a calcareous flush at the neutral end of the soil spectrum through grasslands dominated by *Festuca ovina* or *Nardus stricta*, to rush (*Juncus squarrosus)*, sedge (*Eriophorum* spp.) and dwarf shrub *Calluna vulgaris, Erica tetralix* or *Empetrum nigrum*-dominated vegetation on blanket bog (least productive). Exact locations and plot details are shown in Table 1 and Supporting Information (Fig. S1).

All experiments consisted of paired plots with one from each pair being fenced to exclude sheep and the other left open to allow free range grazing. Sheep grazing densities were estimated during the International Biological; Program in the late 1960s (Table 1, Rawes and Welch, 1969). Throughout, point-quadrats were used to measure species abundance: in all experiments the point-quadrat frame was positioned using a permanently marked reference system within the plot. The sampling positions were selected randomly at the outset. On many occasions height-stratified pins (0–10 cm, 10–20 cm, 20–30 cm and >30 cm) were used to record vascular plants to provide information on canopy composition. The exact way in which the pin frame was used has varied between experiments and on different sampling occasions. For example, not all pins were sampled on every occasion, or only a selection of pins was sampled on a height-stratified basis. Full details of the pin frame technique are given in Marrs et al. (1986) and a summary of the historical sampling information for each experiment is detailed in the Supporting Information Appendix (Table S1).

2.2. Data preparation

The dataset is voluminous and complex and required a substantive pre-processing, first to bring species nomenclature to the same standard: Stace (2010) for vascular plants, Atherton et al., 2010 for bryophytes and Dobson (2000) for lichens, and second to combine some taxa that were recorded inconsistently. These changes are outlined in the Supporting Information. (Table S2).

Whilst all data collection within each experiment was internally consistent, there were differences in methods of stratified random sampling between experiments. Accordingly, the following procedure was adopted to achieve a common recording methodology and intensity across all experiments:

1. All species hits per pin from all height strata were summed to provide pin totals.
2. These summed values were converted to presence/absence data using the 'decostand' function in the 'vegan' package (Oksanen, 2011). Taken together, these two steps reduced all data collected at a single pin to either 1 or 0.
3. The sum of all presences was calculated at each sampling position; depending on the experiment, this was either a pin-frame position or a 1 m^2 quadrat where various positions were sampled. This provided an abundance score of between 0 and 10 for each sampling position for most sites and 0 and 5 for Moss Burn. These data were used in all analyses reported here.

The raw dataset had 139,619 data points; this was reduced to 57,706 and 7830 points by steps 1 and 3 respectively.There were 238 sample variables, 234 species/combined species groups, e.g. *Luzula campestris/multiflora* and four environmental variables (bare rock, bare soil, litter and animal presence (dung/urine noted).

2.3. Data analysis

In order to fit the vegetation within each experiment into a broader UK perspective, a species list for each experiment was collated along with a summed measure of abundance which was then converted to a percentage by dividing by the total number of samples. These data were then passed through TABLEFIT v1.1 (Hill, 1996) to determine the best-fit community according to the National Vegetation Classification (NVC, Rodwell, 1991, 1992). Usually, NVC allocation is achieved using species-abundance scores based on 4 m^2 quadrats for this type of vegetation. This was not possible here, so average species abundance over for the experiment over all years was used instead. It is accepted that this will be a crude approximation.

All other statistical analyses were performed within the R Statistical Environment (R Core Development Team, 2014).

2.3.1. Multivariate analysis

The dataset was analysed with Detrended Correspondence Analysis (DCA) using the 'decorana' function in the 'vegan' package and Hellinger-transformed data; species that were present on only one occasion were removed before the analysis. The correlations between the ordination axes and the five environmental variables (the four noted above plus year) were then calculated using the 'envfit' function (Oksanen, 2011) with 9999 permutations and plotted as passive variables. The distribution of experiments were visualized in ordination space as standard-deviational bivariate ellipses (SD-ellipses, 95% confident limits) using the 'ordiellipse' function (Oksanen, 2011) and centroids of grazing and sheep excluded treatments were then plotted through time for each site.

2.3.2. Univariate analysis

The study design comprised nine sites each with a sheep-grazed and an ungrazed plot. Unfortunately, there was no within-site treatment replication, and hence no way of estimating treatment effects at the site level. Therefore, for each variable we tested for effects of grazing (sheep grazing versus no sheep grazing), time (with Year 0 set to 1955) and their interaction, essentially using the sites as replicates. Species richness and the Shannon–Weiner diversity index were calculated using the 'specnumber' and 'diversity' functions in 'vegan' respectively (Oksanen, 2011). In addition the summed number of hits for each sampling position for eight species groups was computed, i.e. lichens, mosses, liverworts, sedges + rushes, i.e. *Juncus* spp., *Luzula* spp., *Carex* spp., *Eriophorum* spp. and *Trichophorum cespitosum*), sedges (*Carex* spp.), herbs (all dicotyledons), grasses (Poaceae), shrubs (Ericaceae) and all vascular plants.

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Table 1
Description of the nine monitored sheep-grazing exclosures at Moor House NNR in north-west England.

[a]Experiment number	Site name	British National Grid reference	Elevation (m)	[b]Alternative experiment code\Name	Year established	Last year sampled (no. of years of data)	Vegetation type according to (Eddy et al., 1969)	[c]Total area of pure stands of the vegetation types on the Moor House reserve (ha)	[d]Sheep grazing density (sheep ha^{-1})
2	Knock Fell	NY 71794 31267	750	D31	1955	2000 (45)	Limestone Agrosto-Festucetum	125	5.8
3	Hard Hill	NY 72576 33034	690	D40, Hard Hill Ridge	1954	1998 (44)	*Festucetum*	180	2.6
4	Little Dun Fell	NY 70475 33104	830	D42	1954	1998 (44)	*Festucetum*	–	5.8
5	Silverband	NY 71059 30975	690	D34	1966	1997 (31)	Eriophoretum (eroding)	323	0.25
6	Troutbeck Head	NY 72236 31760	690	D30	1966	1997 (31)	Eriophoretum	419	0.5
7	Bog Hill	NY 76789 32869	550	D26	1971	1999 (28)	*Calluna-Eriophorum*	1169	nd
8	Cottage Hill	NY 75801 33641	550	D20, J1, *Juncus* experiment	1967	1995 (25)	*Juncus squarrosus* grassland	373	1.4
9	River Tees	NY 74796 34485	550	D33, N1,Nardus experiment	1967	1995 (25)	*Nardus stricta* grassland	416	2.8
10	Moss Burn	NY 74553 31632	640	D44, Johnny's Flush	1972	1996 (24)	Calcareous flush	14	nd

[a] Experimental number refers to the Moor House site coding system, experiment 1 is the Hard Hill Sheep grazing and prescribed burning experiment which has a different experimental design to those described here (see Lee et al., 2013a for full details).

[b] Various names have been used over the monitoring period, these are reported here for completeness and for cross comparison with earlier work.

[c] The total area of these communities makes up 3019 ha, i.e. 79% of the reserve area of 3842 ha, the remaining vegetation comprised predominantly re-colonising peatland, Sandstone scree and mosaics of the above vegetation classes (Eddy et al., 1969).

[d] Sheep grazing density was determined by dropping volume measurement (Rawes and Welch, 1969); data were not available for two sites (nd).

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Except for vascular plants (no zero counts), the response of each species group to grazing treatment, year and their interaction was modelled using mixed-effects hurdle Poisson regression. Hurdle models are a class of two-part, discrete mixture-models that operate under the assumption that zeroes in the data occur due to a single process whilst a different process drives the non-zero counts (Mullahy, 1986). The first or *hurdle* part of the model estimates the probability of a non-zero count occurring (i.e. whether a guild was present or not), while the second or *count* part of the model relates to the non-zero count distribution (the change in abundance of a species group where it is present). Hurdle Poisson regression was deemed a suitable approach because, (1) the data for all response variables except species richness and vascular plant abundance exhibited a high degree of zero-inflation, and (2) the models allowed for the presence of each vegetation type in response to the predictors (grazing treatment, year and their interaction) to be investigated independently of the vegetation dynamics when that vegetation type was present. As we were interested in broad-scale patterns of change across the moorland, site was specified as a random effect in all models. The models were implemented using the 'MCMCglmm' function in the MCMCglmm v.2.16 package (Hadfield, 2010). Conducting the analyses in a Bayesian framework was deemed the most suitable approach because the data exhibited high levels of over-dispersion, which is readily accounted for during the Bayesian sampling process, and robust 95% confidence intervals could be calculated during posterior sampling, negating the requirement for *post-hoc* bootstrapping. Parameter-expanded priors allowing for random slopes for site and assuming unequal variance were incorporated into all models which allowed for estimation of between site-correlation in both the hurdle and the count parts of the models. The models were run for a 10×10^4 generation burn-in with sampling every 500th iteration for a further 2×10^6 iterations, giving an effective sample size for each parameter estimate of approximately 4×10^4 from the posterior distribution. Model convergence was assessed through inspection of the trace plots. Vascular plants, species richness and Shannon–Weiner diversity were modelled using GLMMs with the same fixed and random effects as the hurdle models.

3. Results

3.1. The individual experiments in the moorland context

The nine experiments covered eight NVC plant community types (Table 2) ranging from blanket bog mire communities (M19, M20), upland grasslands (U5, U6), an upland heath community (H19), calcareous grassland (CG10) and a flushed community (M38). All of the communities showed a high goodness-of-fit for compositional satisfaction but a lower value for mean constancy, implying that a reasonable number of the constant species were present, but the vegetation is relatively species-poor (Hill, 1996). There was a discrepancy (Table 2) between the original description of Festucetum for Hard Hill and Little Dun Fell (Eddy et al., 1969) which was classified as H19 (*Vaccinium myrtillus-Cladonia arbuscula* heath: *Festuca ovina-Galium saxatile* sub-community). The vegetation at both sites included all four of these species; *Festuca ovina*, *Galium saxatile* and *Cladonia arbuscula* are dominants; *Vaccinium myrtillus* is present, but less abundant.

The DCA analysis produced eigenvalues of 0.621, 0.457, 0.363, 0.222 and gradient lengths of 6.33, 5.42, 4.45, 3.96 for the first four axes. The distribution of species shows two clear gradients (Fig. 1a and b). On the first axis the vegetation is dominated by dwarf shrubs (*Calluna vulgaris* and *Empetrum nigrum*) at the negative end, through dwarf-shrub and graminoid-dominated communities (*Vaccinium myrtillus*, *Deschampsia flexuosa*, *Festuca ovina*, *Eriophorum vaginatum* and *Agrostis capillaris*) communities to vegetation with *Luzula* spp., *Deschampsia cespitosa*, *Eriophorum angustifolium*, *Carex nigra* and *Carex demissa*. The second axis reflects a moisture gradient from grassland dominated by *Agrostis capillaris* and *Festuca ovina* through to vegetation dominated by *Empetrum nigrum* and *Eriophorum* spp.

The sites show three clear groupings and a transitional one (Fig. 1c and d): (a) Moss Burn flush which is clearly separated from the others, (b) the hilltop grasslands (Hard Hill, Little Dun Fell, Knock Fell), (3) blanket-bog communities (Bog Hill, Silverband and Troutbeck Head), and (d) the *Juncus*- and *Nardus*-grasslands (Cottage Hill and River Tees) was located between groups (b) and (c). There is little overlap between groups a, b and c, but group d overlaps with groups b and c. The sites show considerable intra-group overlap. The blanket bog sites are at the negative end of the first axis with a relatively low species richness and this increases through the grasslands to the species-rich mire at Moss Burn at the positive end (Fig. 1c and d). The second axis reflects a gradient from the hilltop grasslands (Hard Hill, Little Dun Fell) at the negative end to the remaining sites which occupy positions around the centre of the axis towards the positive end.

The correlations with the environmental variables had relatively low, but significant, r^2 values (Year = 3.1%, $P < 0.001$; Bare rock = 9.2%, $P < 0.001$; Bare soil = 11.6%, $P < 0.001$; Litter = 22.1%, $P < 0.001$; Dung/urine = 0.2%, $P < 0.01$).These variables show a gradient parallel to the second axis (Fig. 1e), reflecting increasing amounts of bare rock and dung/urine on the hilltop grassland communities with greatest sheep grazing pressure (negative end) through the *Juncus*- and *Nardus*-dominated grasslands to the blanket bog communities (positive end) with greater litter and bare soil. The second axis was also correlated positively with sampling year indicating a temporal positive movement.

The temporal trajectories based on the treatment × time centroids (Fig. 2) show relatively little overall movement away from the start position in most sites and considerable fluctuations. However, there was divergence over time between the sheep grazed and ungrazed plots in eight of the sites, the exception being the River Tees site where the two treatments intermingle. The largest movement from the grazed sites is in the *Juncus squarrosus*-dominated grassland (Cottage Hill). At two sites the trajectories were in more or less the same direction (River Tees and Knock Fell), at all others there was either divergence (Bog Hill, Moss Burn and Little Dun Fell) or movement in opposite directions (Silverband, Troutbeck Head, Cottage Hill and Hard Hill).

3.2. Change in species richness, diversity and abundance of species groups

The results from these analyses are complex, the statistical outputs are presented in full in Table S.3 (Supplementary materials), and in summary form in Table 3. The results from both parts of the hurdle models need to be viewed in context of the modelled output (Figs. 3 and 4). The estimates of interest here are the change in the measured variable with respect to time within the sheep-grazed treatment (the intercept): where Year was significant then there was a significant increase (a "Winner", where the estimate was +ve), or decrease through time (a "Loser", where the estimate was −ve). Where a significant enclosed (no-sheep-grazing) × year interaction was detected, there was a significant increase or decrease in this rate of change with respect to the sheep grazed treatment, and this represents a significant effect of no-sheep grazing.

3.2.1. Change in probability of occurrence (hurdle model, part 1)

The change in the probability of occurrence (binomial model, Table 3; Fig. 3) reflects a change in the point-sampled presences and shows that two types of temporal response were detected

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Table 2
The National Vegetation Classification (NVC, Rodwell, 1991, 1992) communities found at each of the nine experiments at Moor House NNR in north-west England. The NVC classes were computed using TABLEFIT (Hill, 1996); the best fit classes are presented along with the goodness-of-fit for compositional satisfaction and mean constancy, plus the overall means derived from four indices (G1–G4).

Site name	NVC class	Mean (G1–G4)	Compositional satisfaction (%) G1	Mean constancy (%) G2	Community description
Bog Hill	M19	68	100	30	*Calluna vulgaris-Eriophorum vaginatum* blanket mire
Cottage Hill	U 6b	61	88	25	*Juncus squarrosus-Festuca ovina* grassland: *Carex nigra-Calypogeia trichomanis* sub-community
*Hard Hill	H19a	61	100	32	*Vaccinium myrtillus-Cladonia arbuscula* heath: *Festuca ovina-Galium saxatile* sub-community
Knock Fell	CG10	55	91	16	*Festuca ovina-Agrostis capillaris-Thymus praecox* grassland
[a]Little Dun Fell	H19a	63	100	30	*Vaccinium myrtillus-Cladonia arbuscula* heath: *Festuca ovina-Galium saxatile* sub-community
Moss Burn	M38	57	96	44	*Cratoneuron commutatum-Carex nigra* spring
River Tees	U 5	73	100	28	*Nardus stricta-Galium saxatile* grassland
Silverband	M20b	71	100	36	*Eriophorum vaginatum* blanket and raised mire: *Calluna vulgaris-Cladonia* spp. sub-community
Troutbeck Head	M20b	73	100	39	*Eriophorum vaginatum* blanket and raised mire: *Calluna vulgaris –Cladonia* spp. sub-community

[a] The description of Festucetum (Table 1) derived from Eddy et al. (1969) does not correspond well with H19a; but they state in their paper "As mentioned in Rawes and Welch (1964) the *Festuca* grasslands are probably more closely related to the Cladineto-Vaccinetum and Festuceto-Vaccinetum, asscociations of McVean & Ratcliffe (1962)". Extracting and fitting the seven Festucetum relevées of Eddy et al. (1969) to NVC class using TABLEFIT resulted in four being allocated to U6c (*Juncus squarrosus-Festuca ovina Vaccinium myrtillus* community; Means of G1 = 87%, G2 = 73%), and one each to U1a (*Festuca ovina-Agrostis capillaris-Rumex acetosella Cornicularia aculeata-Cladonia arbuscula* sub-community; G1 = 87%, G2 = 73%), U1e (*Festuca ovina-Agrostis capillaris-Rumex acetosella Galium saxatile-Potentilla erecta* sub-community; G1 = 87%, G2 = 73%) and H19a (*Vaccinium myrtillus-Cladonia arbuscula* heath Typical sub-community; G1 = 80%, G2 = 60%).

for all of the eight groups tested. In the sheep-grazed plots, the probability of occurrence of grasses, herbs, mosses and sedges all increased through time, whereas lichens and liverworts decreased. Removal of sheep grazing had: (1) no additional significant effect on the probability of occurrence of grasses, lichens and sedges, but (2) a significant additional effect on the rate of change in the probability of occurrence of herbs, mosses (both increasing faster), and liverworts (decreasing faster). Sedges + rushes and shrubs showed no significant change in probability of occurrence through time in the grazed plots, but a small significant increase with no-grazing.

3.2.2. Change in abundance and biodiversity indices (hurdle model, part 2)

The change in the diversity measures and the abundance of the groups (count model) are presented in Table 3 and Fig. 4. Species richness decreased under sheep-grazing. There was no additional

Table 3
Direction of significant change in diversity indices and guilds in a suite of nine experiments at Moor House NNR, north-west England; change in both probability of occurrence and abundance are shown. The full results of the statistical analysis are presented in Table S4 (Supplementary materials) and graphically in Figs. 3 and 4, but all changes noted here (Winners = +ve; Losers = –ve) are significant at $P < 0.05$. The sheep grazing treatment was the intercept in the analysis and the direction of its change is presented; the no-sheep-grazing treatment reflects and additional change in rate. Code: na = not applicable.

Variable	Probability of occurrence		Abundance	
	Grazed	Ungrazed	Grazed	Ungrazed
Species richness	na	na	−ve	−ve, same
Shannon–Weiner	na	na	No change	+ve
Vascular plants	na	na	−ve	−ve, same
Sedges + rushes	No change	+ve	No change	No change
Shrubs	No change	+ve	+ve	+ve, faster
Lichens	−ve	−ve, same	−ve	−ve, slower
Liverworts	−ve	−ve, faster	−ve	−ve, faster
Herbs	+ve	+ve, faster	+ve	+ve, same
Grasses	+ve	+ve, same	−ve	−ve, faster
Mosses	+ve	+ve, faster	−ve	+ve
Sedges	+ve	+ve, same	+ve	+ve, faster

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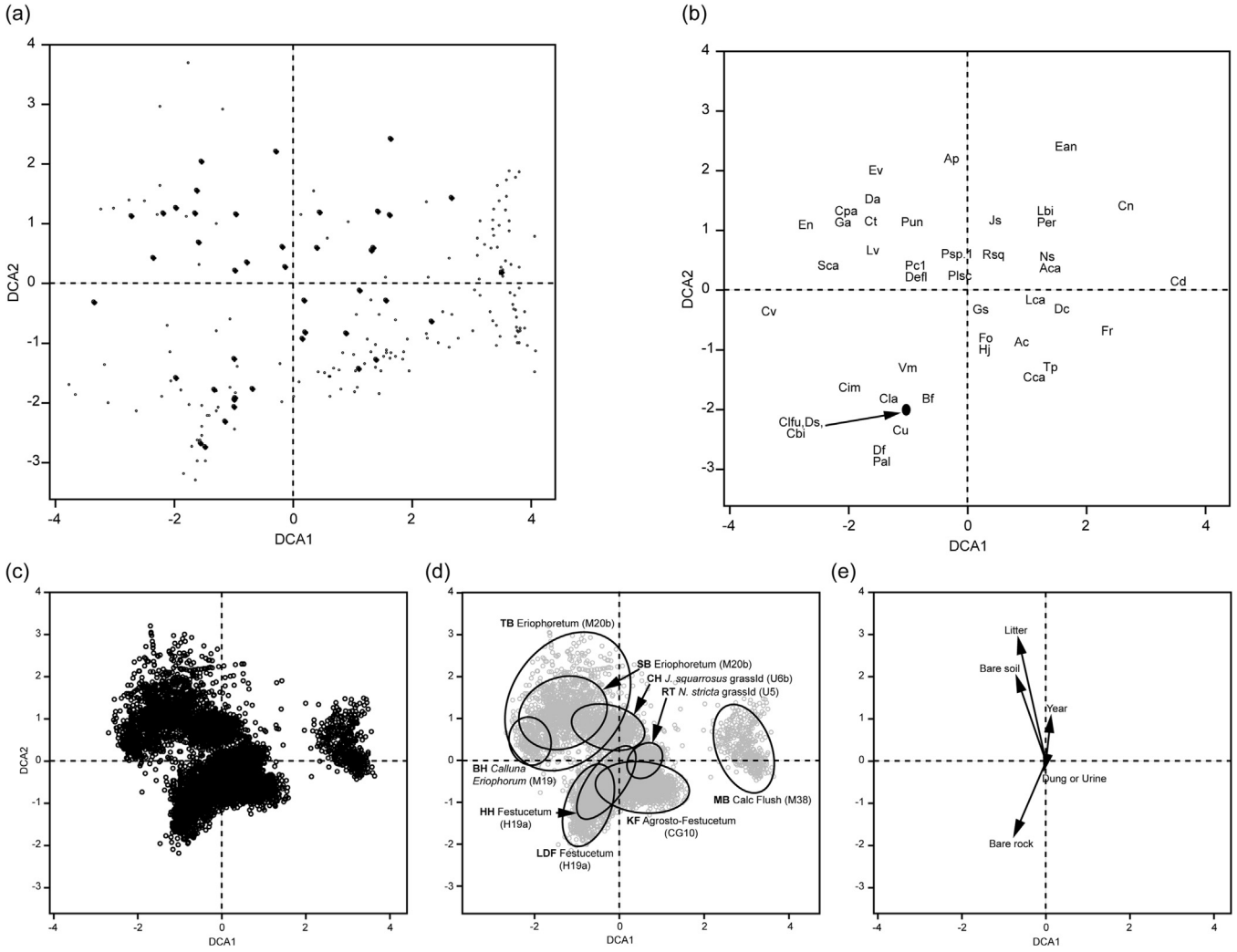

Fig. 1. Plots derived from the DCA analysis of plant species composition data within nine experiments investigating the effects of sheep-grazing versus no sheep grazing at Moor House NNR, north-west England: (a) Species plot, all species are illustrated (large dots = the most abundant species); (b) Species plot showing only the most abundant species (species with more than 500 presences in the database (max = 35,199 for *Festuca ovina*); this encompassed 23% of the total number of species); (c) the distribution of sampling units; (d) the distribution of the nine experiments in ordination space illustrated using bivariate SD-ellipses (95% confidence limits) superimposed; (e) the significant environmental variables correlated with the ordination. Species codes for (b): Ac = *Agrostis capillaris*, Aca = *Agrostis canina*, Ap = *Aulacomnium palustre*, Bf = *Barbilophozia* spp, Cbi = *Carex bigelowii*, Cca = *Carex caryophyllea*, Cd = *Carex demissa*, Cim = *Cladonia impexa*, Cla = *Cladonia arbuscula*, Clfu = *Cladonia furcata*, Cn = *Carex nigra*, Cpa = *Campylopus paradoxus*, Ct = *Calypogeia* spp, Cu = *Cladonia uncialis*, Cv = *Calluna vulgaris*, Da = *Diplophyllum albicans*, Dc = *Deschampsia cespitosa*, Defl = *Deschampsia flexuosa*, Df = *Dicranum fuscescens*, Ds = *Dicranum scoparium*, Ean = *Eriophorum angustifolium*, En = *Empetrum nigrum*, Ev = *Eriophorum vaginatum*, Fo = *Festuca ovina*, Fr = *Festuca rubra*, Ga = Green algae, Gs = *Galium saxatile*, Hj = *Hypnum jutlandicum*, Js = *Juncus squarrosus*, Lbi = *Lophocolea bidentata*, Lca = *Luzula campestris\multiflora*, Lv = *Lophozia* spp, Ns = *Nardus stricta*, Pal = *Polytrichum alpestre*, Pc1 = *Ptilidium ciliare*, Per = *Potentilla erecta*, Plsc = *Pleurozium schreberi*, Psp 1 = *Polytrichum* sp, Pun = *Plagiothecium undulatum*, Rsq = *Rhytidiadelphus squarrosus*, Sca = *Sphagnum capillifolium*, Tp = *Thymus praecox\arcticus*, Vm = *Vaccinium myrtillus*. Site codes for (d): BH = Bog Hill, CH = Cottage Hill, HH = Hard Hill, LDF = Little Dun Fell, KF = Knock Fell, MB = Moss Burn, RT = River Tees, SB = Silverband, TB = Troutbeck Head.

effect under the no-sheep-grazing treatments, though the enclosed plots had a significantly lower starting value. There was no change in Shannon–Weiner diversity through time in the grazed treatments, whilst a small but significant increase though time was found in the ungrazed plots.

Three groups showed an increase in abundance through time in the grazed plots (herbs, sedges and shrubs); removal of sheep grazing had no significant additional effect on the abundance of herbs but significantly enhanced the rate of increase of sedges and shrubs. All other groups except for sedges + rushes declined through time in the sheep-grazing treatment; the sedges + rushes showed no change. Enclosure produced slower rates of decrease for lichens, but faster rates of decrease for grasses and liverworts, no additional effects for vascular plants, whilst for mosses, enclosure resulted in a reversal of the trajectory found in the grazed treatment (Fig. 4).

4. Discussion

4.1. Problems associated with the analysis of long-term plant community data

There are always problems in analysing data from long-term experiments (Lee et al., 2013a), because the experiments often do not begin as long-term studies and insufficient thought may have been given to their experimental design, recording methods and data storage at the outset. Here, even though the experiments all had the same experimental design (sheep-grazed-plot versus no-sheep-grazing) and the same monitoring methods (Marrs et al., 1986; Adamson and Kahl, 2003), the experiments started in different years and comparable measures were not always made simultaneously in both plots at the outset. Accordingly, some time elapsed between setting up the experiments and the first set of

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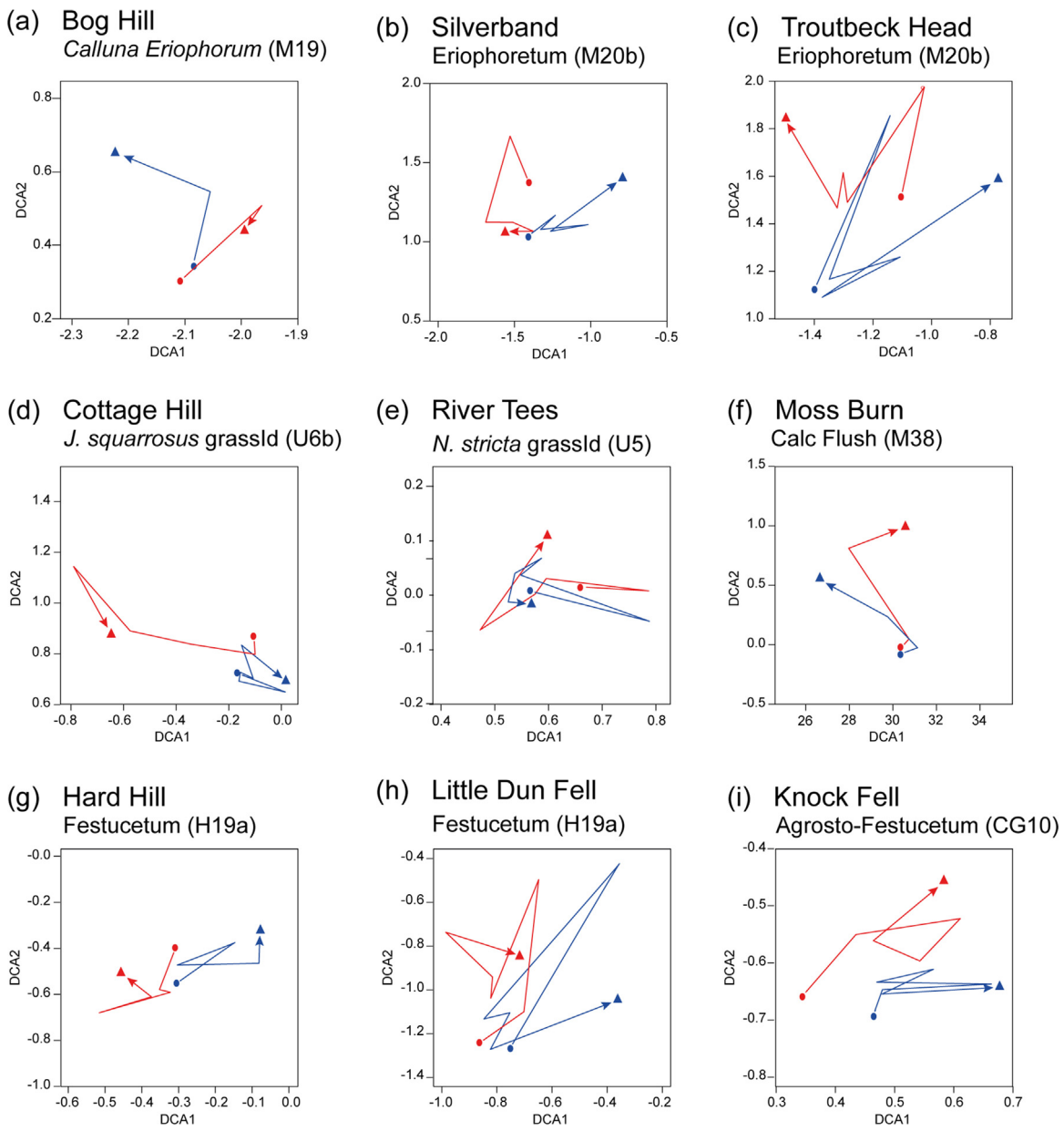

Fig. 2. Successional trajectories in both the sheep-grazing (blue) versus no sheep grazing treatments (red) in nine experiments at Moor House NNR, north-west England. The start positions are denoted with circles and the end positions with diamonds. This plot is of the treatment × time centroids from the DCA analysis (Fig. 1); each panel has been scaled to reflect similar dimensions on both axes.

comparable data. As a result immediate changes in vegetation because of enclosure can only be inferred and probably explain the differences observed here between the treatments. Accordingly, we have not discussed these differences here; rather we have concentrated on the rates of change through time.

Two other issues needed to be tackled. The first was species nomenclature with respect to name changes through time and the likelihood of different recording teams identifying critical groups to differing standards. This was tackled using a clean-up procedure (Table S2, Supplementary materials), and for this study at least, the calculation of total abundance of high-level taxonomic\physiognomic groups. Misnaming and misidentification errors should, therefore, be relatively low. The second issue was that whilst the basic recording methodology was similar throughout, some measurements were made using counts of all species touches on height-stratified pins and some were first-touch species presences only (Marrs et al., 1986). Therefore, all of the data had to be converted to a "single unit of currency", namely the number of presences on either a 10-point pin frame or within a series of pin positions within a 1 m^2 quadrat.

4.2. The range of variation covered by the experiments

In any monitoring of species change within a given resource it is essential to encompass a reasonable range of the variation within the reserve. Here, the nine experiments were established on eight different community types within the British National Vegetation Classification (Rodwell, 1991, 1992), and accordingly fulfilled the intention of providing information on species change across the spectrum of plant communities described at Moor House. There was a discrepancy between the description of Festucetum of Eddy et al. (1969) and the NVC class fitted here – the *Vaccinium myrtillus-Cladonia arbuscula* heath (*Festuca ovina-Galium saxatile* sub-community). We suspect that the term Festucetum was a

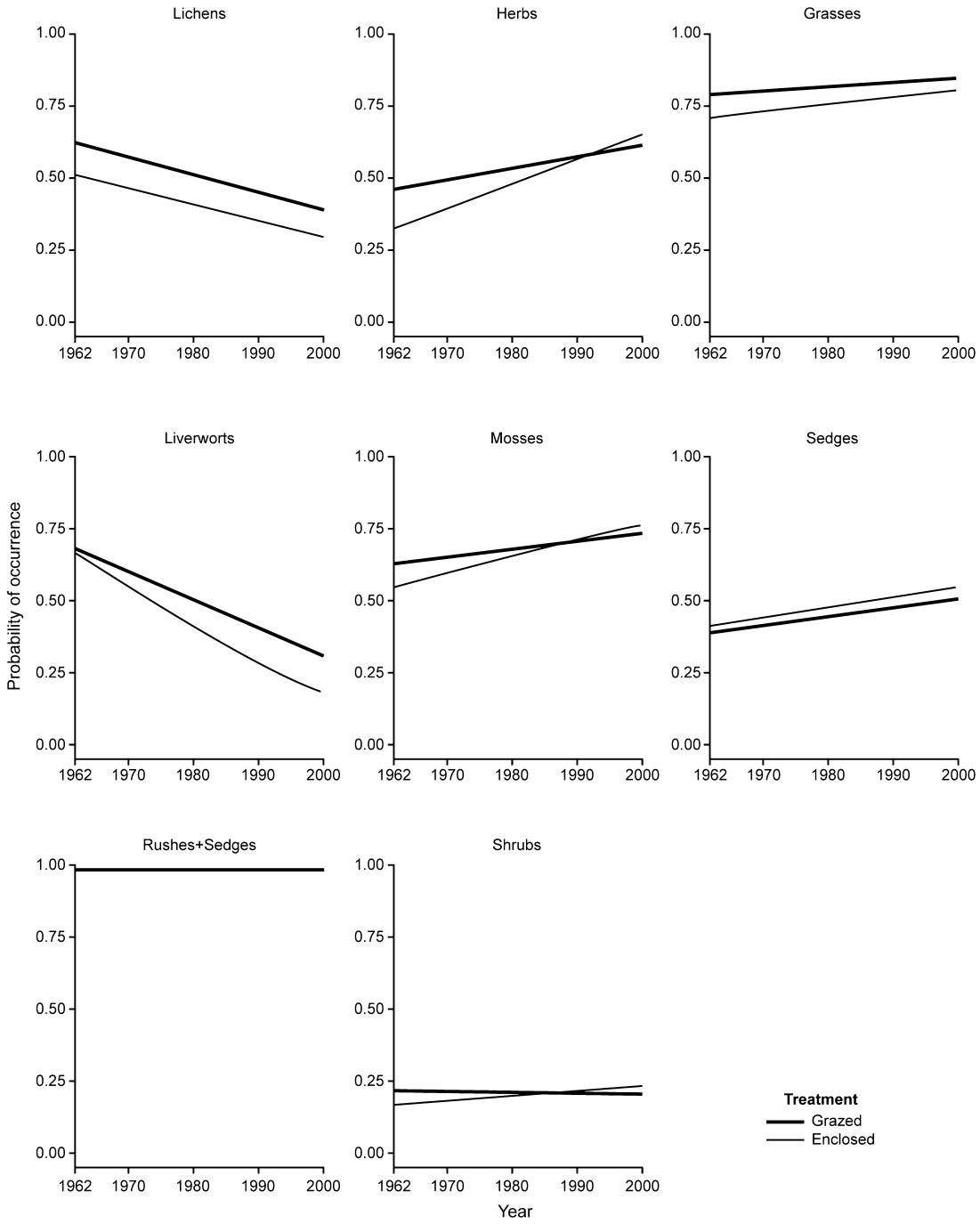

Fig. 3. Fitted modelled responses of the probability of occurrence of selected guilds through time within nine experiments investigating the effects of sheep-grazing versus no sheep grazing at Moor House NNR, north-west England. Full outputs (Binomial part of the hurdle models) are presented in Table S3 (Supplementary materials).

fairly coarse description as re-analysis of their relevées produced four NVC community/sub-communities including the *Vaccinium myrtillus-Cladonia arbuscula* heath one (Table 2).

The vegetation across the nine experiments was separated on two gradients, the first separating the base-rich flush (Moss Burn) from the other eight (x-axis, Fig. 1); these eight were then separated on a climate-soil type gradient (y-axis, Fig. 1). Surprisingly, there was relatively little change through time within the experiments suggesting that the communities were relatively stable, although there was divergence between the sheep-grazed and ungrazed plots in eight of the nine experiments. The exception was the River Tees site which was noted as relatively stable in an earlier analysis (after ten years, Rawes, 1981), and it is remarkable that this stability has persisted over a 29-year period.

The distribution of sites within the ordination suggested four experiment-subsets, even though there was considerable amount of within-group overlap (Fig. 1). The groups were:

a. Blanket Bog sites ($n = 3$: Bog Hill, Silverband, Troutbeck Head),
b. Transitional grasslands ($n = 2$: Cottage Hill, River Tees),transitional group between (a) and (c),
c. High-level grasslands ($n = 3$: Hard Hill, Little Dun Fell, Knock Fell), and
d. Base-rich flush ($n = 1$: Moss Burn).

Previous analyses have considered change in vegetation at the individual experiment level (Rawes, 1981, 1983; Marrs et al., 1988). For the first three sub-sets we suggest that any future analyses of

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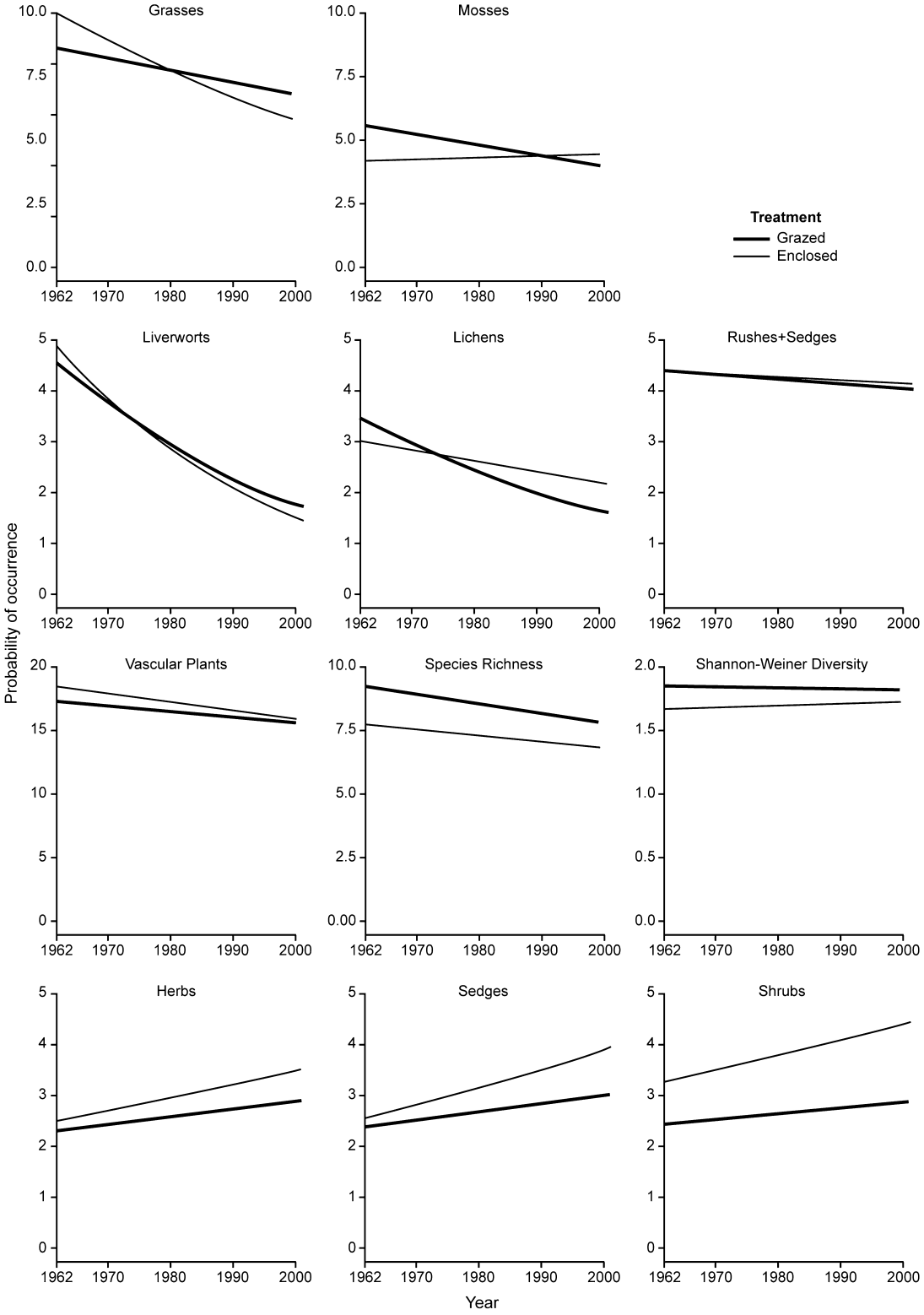

Fig. 4. Fitted modelled responses of (1) the abundance of selected guilds, and (2) species richness and the Shannon–Weiner Index through time within nine experiments investigating the effects of sheep-grazing versus no sheep grazing at Moor House NNR, north-west England. Full outputs (Count part of the hurdle models) are presented in Table S3 (Supplementary materials).

change in individual species through time should be carried out on pooled data with the experiments within-group treated as replicates. This would provide a greater degree of statistical rigour than previous analyses. This structure was to some extent planned as experiments within the subsets tended to be monitored in the same year. Moss Burn, a relatively base-rich site (Marrs et al., 1988), has no obvious replicate and can only be analysed independently as a case-study.

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4.3. Analytical methodology for assessing change in species groups through time

Although mixed-effects hurdle models have been shown to be powerful tools in ecology (Potts and Elith, 2006), they are seldom-used. One reason might be due to the inherent difficulty in assessing the providence of zero counts within the data. Here, it was reasoned a priori that zeroes within the counts were true zeroes due to the low taxonomic resolution at which the species groups were recorded, i.e. species misclassification would be unlikely at the taxonomic resolution used here. Moreover, the Bayesian approach to analysis allowed for all data to be analysed without transformation (O'Hara and Kotze, 2010) whilst also accounting for over-dispersion. The resultant analyses allowed for two subtly distinct processes to be modelled; (1) the effects of grazing and time on the probability of a species group occurring, and (2) if a vegetation group was present, the effects of grazing and time on the abundance of that species group. Thus, information was obtained on both the change in probability of a species group being present or not, and any change in its abundance. These two analyses provide information on two different parts of the change in abundance of species, both relevant for conservation managers and policy-makers.

4.4. Changes in species richness, diversity and species groups through time

The null hypothesis of no change through time in the sheep-grazed treatment was rejected, as there was an overall decrease in species richness through time, though the Shannon–Weiner diversity index showed no change. Interestingly, whilst species richness was found to decrease at the same rate in both the grazed and ungrazed treatments, diversity was found to increase in the ungrazed treatment. However, the ungrazed treatment started at a lower value for these variables than the sheep-grazed plots and this probably reflects a reduction in species in the period immediately after the start of the experiment and the first comparable dataset available for each treatment (see above).

Within the sheep-grazed treatment, the changes in both the probability of occurrence (i.e. number of point sources on the ground) and abundance identified both temporal changes and potentially different effects between the groups in how these changes occurred. In terms of the probability of occurrence, two species groups (lichens and liverworts) showed a reduction in point presences, i.e. these groups were present at fewer points on the ground as time progressed, whilst with exception of sedges + rushes, all other groups increased. However, when abundance was considered herbs, sedges and shrubs increased through time and all groups other than sedges + rushes (no change) were reduced. Taken together, these results suggest a directional change (hypothesis 2 accepted) and that the vegetation is losing some species groups through time under "business-as-usual" grazed conditions, which along with the overall reduction in species richness supports the biotic homogenization hypothesis. Lichens and liverworts were particularly vulnerable as they are reducing in both occurrence and abundance.

The effects of removal of sheep-grazing led to additional increases in the probability of occurrence of herbs, mosses and shrubs, and a greater reduction in liverworts. Sedges + rushes showed little change in probability of occurrence, except for a slight increase in the enclosed treatment. The abundance data showed the rate of decrease slowing for lichens and accelerating for many of the other species groups (grasses, liverworts and vascular plants). Overall, removal of sheep grazing had some positive effects (increased diversity and increased sedges + rushes, herbs, mosses and sedges, but some negative ones (Hypothesis 3 partially accepted).

One of the drawbacks of analysing these data as species groups is that it masks the effects of changes in individual species; for example any increase within a group might result from the increase of just one dominant species. As an example, one of the few favourable results from exclosure was the increased moss abundance. Without analysis of species composition data it is difficult to determine whether the increases in this group can be construed as favourable or not, i.e. abundance may be increasing at group level, but the composition of the species within the group may be changing in a undesirable way, with the diversity decreasing and the abundance increases driven by one, or a few, species. This can be clarified by future analyses at species level within the site-subsets noted above.

Previous analyses of these experiments have concentrated on species change within the enclosures and little attempt has been made to relate them to the ongoing, parallel changes occurring in the sheep-grazed enclosures (Rawes, 1981, 1983). Rawes concentrated on changes in individual species and general trends generally reflect those reported here for species-groups, i.e. for blanket bog (increasing shrub abundance increased, liverworts reduced) and grasslands (sedge and selected bryophytes abundance increased and rushes reduced (predominantly *Juncus squarrosus*). Reductions in bryophytes and lichens have also been detected in other studies of upland vegetation (Britton and Fisher, 2010; Hall et al., 2011).

4.5. Implications for land managers and conservation

These results indicate a continuing decline in biodiversity value since Moor House was acquired as a nature reserve in 1952 specifically for scientific purposes. The long-term vision of the early conservation scientists who set these, and other, experiments up (Lee et al., 2013a,b), is now yielding important data to help guide nature conservation management. These long-term experimental datasets and allied information, integrates well with the data collected within the UK's Environmental Change Network. The reserve has, over this period, been managed using minimal intervention apart from sheep-grazing and some relatively small-scale experimental treatments (Lee et al., 2013a,b). The research reported here has highlighted several important messages for conservation managers and policy makers.

4.5.1. The current status

There has been a continued decline in species richness and changes in the probability of occurrence and abundance of several species groups since the middle of the 20th century. Of particular concern are the reductions in (1) the probability of occurrence of liverworts and lichens and (2) the abundance of lichens, liverworts, grasses and mosses. These species groups were particularly sensitive to change and as they are relatively easy to identify at the high-scale taxonomic resolution used here, they may provide good indicators of change for use elsewhere. Moreover, the results imply a biotic homogenization of these plant communities with a shift to dominance by the more competitive herbs, sedges, and shrubs. Biotic homogenization has been detected elsewhere in Great Britain at the countrywide-scale (Smart et al., 2006) and within alpine and montane communities (Britton et al., 2009; Ross et al., 2012), and it is possible that this reflects a continuing late-twentieth century impact of atmospheric pollution (Smart et al., 2003a,b; Maskell et al., 2010; Britton and Fisher, 2010; Hall et al., 2011; Armitage et al., 2012). Our results contrast to some extent with those of Rose et al. (2015) who demonstrated an increased species richness across all 12 ECN terrestrial sites between 1993 and 2012. Importantly, this result was derived from values averaged across all 12 sites encompassing a range of broad-habitat types, and was from a later time-frame than examined here, when there was evidence of a reduction in pollutant loads. Moreover, only vascular plants were included in the Rose et al. (2015) study. It will

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be interesting to see if this positive signal identified in the wider study of Rose et al. (2015) will be detected when the next series of monitoring data from the Moor House grazing experiments become available for analysis.

4.5.2. Restoration of what was there at the start

If there is a general wish to restore the plant communities that were present when the Moor House reserve was set up when sheep-grazing pressures and atmospheric pollutant loads were higher than they are currently then clearly some restoration initiatives are needed, almost certainly requiring substantive disturbance treatment (herbicide, fire, physical damage) to create germination safe-sites (Harper, 1977), plus the addition of seed (vascular plants) or spores/fragments (bryophytes and lichens) (Miles, 1974; Lee et al., 2013b; Milligan et al., 2004). The restoration of bryophytes and lichens into extant vegetation is an area where a great deal of experimental information is lacking (Hinde et al., 2010).

4.5.3. Reducing sheep numbers and rewilding

The effect of removal of sheep-grazing was on selected groups but generally the communities were rather stable. This suggests that if sheep numbers are reduced further through predicted changes to the European Union's Common Agricultural Policy (Cole et al., 2010) or through a complete cessation of management in rewilding scheme (Monbiot, 2013; Sandom et al., 2013), the vegetation is unlikely to change much over a 28–44 year period. An increase in shrub abundance was detected but this was not reflected to the same extent in probability of occurrence, suggesting that measured change is through the growth expansion of individuals rather than through recruitment of new plants. This was implied in a previous study of the Cottage Hill *Juncus squarrosus*-dominated grassland where one individual patch of *Calluna vulgaris* had expanded (Marrs et al., 1988). Specifically, there was no evidence of tree invasion and this is probably for at least five reasons: (1) the relatively large distances from sources of both seed and mychorrizae, which would be needed to enable the trees to grow in these soils and (2) lack of disturbance in the exclosures to provide safe-sites for germination (Harper, 1977), (3) the relative small size of the exclosures (maximum size = 900 m^2), (4) the high altitude and (5) unsuitable soil type. Thus, any attempt to change the composition of the vegetation on this reserve by reducing sheep-grazing will, on the basis of these results, take a very long time unless there is some intervention management. However, it could be argued that vegetation change might differ considerably from these small-plot studies if the sheep-grazing pressure were to be reduced over a much larger geographic scale, i.e. the entire reserve. This is possible, but remains to be tested.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2015.10.053.

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